

# Beet Leafhopper (Hemiptera: Cicadellidae) Settling Behavior, Survival, and Reproduction on Selected Host Plants

J. E. MUNYANEZA AND J. E. UPTON

USDA-ARS, Yakima Agricultural Research Laboratory, Wapato, WA 98951

J. Econ. Entomol. 98(6): 1824-1830 (2005)

**ABSTRACT** Experiments were conducted to determine the settling behavior, survival, and reproduction of the beet leafhopper, *Circulifer tenellus* (Baker), when maintained on selected host plants. This leafhopper was recently identified in the Columbia Basin of Washington and Oregon as the probable vector of the beet leafhopper-transmitted virescence agent phytoplasma, causal agent of several vegetable crop diseases, including potato purple top. Plants selected for study were sugar beet, *Beta vulgaris* L.; radish, *Raphanus sativus* L.; dry bean, *Phaseolus vulgaris* L.; potato, *Solanum tuberosum* L.; carrot, *Daucus carota* L.; and tomato, *Lycopersicon esculentum* Mill. Leafhopper adults were confined on caged plants, and settling behavior was observed during a 72-h period and survival was monitored for 40 d. Also, oviposition and nymphal production were investigated by maintaining leafhoppers for  $\approx 90$  d on each of the selected plants. Sixty to 100% of leafhoppers settled on all studied plants during the first 5 h, but settling on bean and tomato declined sharply thereafter. Leafhopper mortality was very high on bean and tomato, with 95 and 65% of the leafhoppers, respectively, dying in about a week. In contrast, 77, 90, and 95% of leafhoppers maintained on potato, sugar beet, and radish, respectively, survived until the end of the 40-d experimental period. Beet leafhopper oviposition and nymphal production and development only occurred on sugar beet, radish, and potato; reproduction was lower on potato.

**KEY WORDS** *Circulifer tenellus*, plant pathogens, settling behavior, survival, reproduction

THE BEET LEAFHOPPER, *Circulifer tenellus* (Baker), is a serious insect pest throughout the western United States. It transmits Beet curly top virus (family *Geminiviridae*, genus *Curtovirus*, BCTV) to several crops and is the only known vector of this destructive plant pathogen (e.g., Thornberry 1966, Cook 1967, Thomas 1969, DeLong 1971). More than 300 plant species are affected by this disease, including beans, *Phaseolus vulgaris* L.; sugar beet, *Beta vulgaris* L.; cantaloupe, *Cucumis melo* L.; cucumber, *Cucumis sativus* L.; pepper, *Capsicum annuum* L.; spinach, *Spinacia oleracea* L.; squash, *Cucurbita maxima* Lam.; tomato, *Lycopersicon esculentum* Mill.; watermelon, *Citrullus lanatus* Thunb.; and several ornamental species (Hills 1937; Cook 1941, 1967; Lawson et al. 1951; Thornberry 1966; Thomas 1969; DeLong 1971; Thomas and Martin 1971; Thomas and Boll 1977; Capinera 2001). Because of this insect pest, production of sugar has been abandoned in several western sugar beet-producing areas and commercial vegetable production is infrequent in some southwestern areas owing to high incidence of BCTV.

The beet leafhopper shows strong preference for some plant hosts over others and tends to accumulate on preferred hosts (Thomas and Martin 1971). However, many of the crops affected by the beet leafhopper-transmitted diseases are less or nonaccepted hosts

and not suitable for survival and reproduction of this leafhopper (Thomas 1972; Severin 1928, 1929). Recently, this leafhopper was found to be the probable vector of the beet leafhopper transmitted virescence agent (BLTVA) phytoplasma, which is the causal agent of several diseases in the Columbia Basin of Washington and Oregon, including the potato purple top and dry bean phyllody diseases (Lee et al. 2004a, b; Crosslin et al. 2005). A pathogen similar to BLTVA phytoplasma has previously been reported on potatoes in Utah (Smart et al. 1993) and Korea (Jung et al. 2003) and on radish seed crops in Idaho (Shaw et al. 1990) and Washington (Schultz and Shaw 1991). The same phytoplasma was found to cause the tomato big bud disease (Shaw et al. 1993) and has been successfully transmitted to >40 host plants in laboratory studies by using the beet leafhopper as vector (Golino et al. 1989), including several vegetable and ornamental crops previously reported as susceptible to BCTV. The beet leafhopper also transmits *Spiroplasma citri* Saglio et al., which causes ailments known as stubborn disease in citrus and brittle root in horseradish (O'Hayer et al. 1984). Mechanisms used by this leafhopper to effectively transmit various pathogens to plants are poorly understood.

Feeding behavior and host suitability and susceptibility play important roles in pathogen transmission

by insect vectors. Rate and duration of feeding greatly influence the outcome of insect-plant interactions (Miller and Strickler 1984), including pathogen transmission. These rates however depend upon insect settling behavior and the amount of time associated with the host (Miller and Strickler 1984; Bernays 1996, 2001). Moreover, Miller and Strickler (1984) pointed out that host plant preference differs from host acceptance because, unlike preference, acceptance does not specify whether alternatives are offered; it simply indicates that consumption (or oviposition) behaviors occur. They also indicated that, in practice, there may be no clear line distinction between acceptance and rejection, particularly when only minimal consumption occurs. In such cases, it may be difficult to distinguish between nibbling primarily for obtaining sensory information from the source, and a low level feeding. However, sustained settling behavior and feeding indicate that the examined plant has been accepted (Miller and Strickler 1984).

Feeding behavior by piercing-sucking plant feeding insects such as leafhoppers usually involves much more complex plant-insect interactions than feeding by herbivores with chewing mouthparts. The complex plant-insect interactions during feeding by piercing-sucking insects occur beneath the plant surface and thus are not directly observable; to overcome limitations with this feeding behavior, the main technique used to study these interactions is the electrical penetration graph (EPG) monitoring (McLean and Weight 1968, Almeida and Backus 2004, Backus et al. 2005). Although the act of feeding by leafhoppers cannot be discerned easily without the EPG device, settling behavior studies are very useful in providing information on the insect handling process that includes host plant examining and consuming activities such as feeding or oviposition (Miller and Strickler 1984).

With the exception of a few comparative studies conducted on BCTV transmission to tomato and sugar beet (Thomas 1972, Thomas and Martin 1971, Thomas and Boll 1977), little is known about the interactions between the beet leafhopper and its less or nonaccepted hosts. This information is essential in formulating strategies to effectively managing pathogens transmitted by this insect pest, including phytoplasmas. The primary objective of the current study was to determine the settling behavior and adult survival of the beet leafhopper maintained on selected host plants to gain understanding of the mechanisms of how this leafhopper species transmits pathogens to plants that are not its accepted hosts. Also, reproductive response of this leafhopper to these selected plants was investigated.

### Materials and Methods

**Sources of Plants and Beet Leafhoppers.** The experiments were conducted in both greenhouse and controlled experimental rooms at the USDA-ARS, Wapato, WA. The plants selected for the study were the sugar beet, *Beta vulgaris* L. variety *Saccherifera*;

radish, *Raphanus sativus* L. variety *Cherry Belle*; dry bean, *Phaseolus vulgaris* L. variety *Le Baron*; potato, *Solanum tuberosum* L. variety *Russet Burbank*; carrot, *Daucus carota* L. variety *Enterprise*; and tomato, *Lycopersicon esculentum* Mill. variety *Brandywine*. These plants were chosen for the study because they are among economically important crops grown in the Pacific Northwest and are often planted in proximity of each other. In addition, all these plant species are known to be susceptible to pathogens associated with the beet leafhopper, including BCTV and the BLTVA phytoplasma; serious outbreaks of these beet leafhopper-transmitted pathogens have recently been observed on these studied crops and are increasingly on the rise in the Pacific Northwest (Munyaneza 2003, 2004a, b; Munyaneza et al. 2005). All the plants used in the current study were grown individually from seed in 4-liter pots (J. W. McConkey, Inc., Summer, WA) in growth chambers (Percival Scientific, Inc., Perry, IA) maintained at 24°C, 50% RH, and a photoperiod of 16:8 (L:D) h. The growth media used consisted of a mixture of four parts peat moss, four parts perlite, one part sand, one part vermiculite, in addition to Osmocote fertilizer and Micromax micronutrients (Scotts Co., Marysville, OH). The growth media pH was adjusted to 6.8 by the addition of dolomite lime to optimize seed germination and growth. After emergence, the plants were placed on a biweekly fertilizer regimen using Peters Professional 20:10:20 Fertilizer (Scotts Co.) at a rate of 2 mg per pot. These plants were in seedling stage when first used in the experiment and their height ranged from 8 to 12 cm. Beet leafhoppers were field collected from weeds in various locations of the Columbia Basin and reared on sugar beet and radish plants in a controlled experimental room for several generations; the room was maintained at 23°C, 50% RH, and a photoperiod of 16:8 (L:D) h.

**Settling Behavior Study.** After starving the insects for 24 h, 10 adults were released on each of the selected plants in a greenhouse maintained at 26°C, 50% RH, and a photoperiod of 16:8 (L:D) h. Each plant was enclosed in an isolation cage. Each isolation cage was made of clear Mylar plastic and consisted of a cylinder (15 cm in diameter, 40 cm in height) and a removable Mylar plastic top, which fits the top of the cylinder. In total, four circular 6-cm-diameter vents were placed in the cage; three of the vents were located equidistant around the lower one-third of the cylinder, and one was located in the removable top. The vents were screened with organdy cloth to allow ventilation in the cage and to prevent insect escape. The cage was designed to fit tightly inside the rim of the 4-liter greenhouse pots. Settling behavior studies were conducted similarly to techniques used by Thomas and Martin (1971), Thomas (1972), and Thomas and Boll (1977) to study host preference of the beet leafhopper, but with some modifications. After release, the beet leafhoppers were given time to settle down on the plant and adjust to the caged plant environment and observations started immediately after 1 h and every hour thereafter for 7 h and then after 24, 48, and 72 h.

**Table 1.** Mean percentage ( $\pm$ SEM) of beet leafhopper adults settling on selected host plants after being confined on caged plants for 1, 2, 3, 4, 5, 6, 7, 24, 48, and 72 h

Host plant	Hours of exposure									
	1	2	3	4	5	6	7	24	48	72
Sugar beet	92 $\pm$ 2.0ab	100 $\pm$ 0.0a	96 $\pm$ 2.4a	100 $\pm$ 0.0a	100 $\pm$ 0.0a	100 $\pm$ 0.0a	100 $\pm$ 0.0a	100 $\pm$ 0.0a	96 $\pm$ 4.0a	100 $\pm$ 0.0a
Radish	100 $\pm$ 0.0a	100 $\pm$ 0.0a	100 $\pm$ 0.0a	100 $\pm$ 0.0a	98 $\pm$ 2.0a	96 $\pm$ 2.4a	100 $\pm$ 0.0a	100 $\pm$ 0.0a	100 $\pm$ 0.0a	98 $\pm$ 2.0a
Potato	70 $\pm$ 7.1bc	90 $\pm$ 4.5b	90 $\pm$ 3.1a	100 $\pm$ 0.0a	90 $\pm$ 3.1ab	96 $\pm$ 2.5a	96 $\pm$ 4.0a	100 $\pm$ 0.0a	100 $\pm$ 0.0a	90 $\pm$ 3.1ab
Carrot	80 $\pm$ 5.5bc	70 $\pm$ 4.5c	86 $\pm$ 6.0a	82 $\pm$ 3.8b	96 $\pm$ 2.6ab	90 $\pm$ 4.5ab	100 $\pm$ 0.0a	90 $\pm$ 3.1b	90 $\pm$ 4.5a	80 $\pm$ 5.5b
Tomato	76 $\pm$ 5.1bc	100 $\pm$ 0.0a	80 $\pm$ 7.0a	80 $\pm$ 3.1b	80 $\pm$ 6.3bc	70 $\pm$ 5.5bc	70 $\pm$ 4.5b	66 $\pm$ 4.0c	60 $\pm$ 5.5b	50 $\pm$ 8.4c
Dry bean	60 $\pm$ 8.9c	86 $\pm$ 2.4bc	80 $\pm$ 7.1a	86 $\pm$ 5.1b	60 $\pm$ 7.1c	50 $\pm$ 6.3c	60 $\pm$ 3.1b	56 $\pm$ 2.4c	50 $\pm$ 5.5b	40 $\pm$ 7.0c

Means followed by the same letter within columns are not significantly different ( $P > 0.05$ ; Bonferroni  $t$ -tests).

Each observation lasted 20 min during which the numbers of leafhoppers on the plant and cage wall were recorded. Each experiment was replicated five times for each of the selected plants; a new plant and set of 10 insects were used for each replicate.

**Adult Survival Study.** Adult survivorship was investigated using an environmentally controlled room also maintained at 23°C, 50% RH, and a photoperiod of 16:8 (L:D) h. Beet leafhoppers nymphs were collected from the laboratory colony and placed in a large cage containing sugar beet plants. Newly emerged beet leafhopper adults (1–6 d old) were collected from the emergence cage, and 20 leafhoppers were confined on each of the selected plants. The plants were enclosed in an isolation cage as previously described and used only once. The experiment was replicated eight times for each plant species. Population level of leafhopper survival was recorded at 1, 2, 4, 7, 9, 12, 14, 17, 20, 25, 30, and 40 d by counting number of leafhoppers alive. At each census, leafhoppers were counted by placing and shaking each plant in a light box, prompting leafhoppers to fly to the wall of the box. After recording the number of leafhoppers present in the light box for each plant, the insects were collected again using an insect aspirator and returned to the caged plant. The counting was discontinued after 40 d because of the production of nymphs on some of the experimental caged plants. At this time, it was concluded that these nymphs were about to turn into adults, which would have confounded results and made it impossible to accurately account for the leafhoppers originally involved in this specific experiment.

**Reproductive Response Study.** Oviposition and nymphal production and development were investigated by maintaining 25 beet leafhopper adults (15 females and 10 males) on each of the selected plants enclosed in the isolation cages as described previously. Eight replications were conducted for each of the selected plants. The caged plants with the beet leafhoppers were maintained in a controlled rearing room maintained in similar conditions as for the survival experiment. The plants were checked for oviposition and nymphal production weekly. Oviposition was checked by visually inspecting leaves for oviposition sites and dissecting one to three leaves per plant for eggs weekly. Oviposition and nymphal production were monitored for  $\approx$ 90 d or until plant senescence or the death of all leafhoppers.

**Statistical Analysis.** Data were analyzed using SAS 9.1 for Windows (SAS Institute 2003). Repeated measures analysis of variance (ANOVA) was used to test for differences in settling behavior on the selected plants after 1, 2, 3, 4, 5, 6, 7, 24, 48, and 72 h. ANOVA was performed after transformation of percentage data by using arcsine square root. The level of significance was set at  $P = 0.05$ ; and to control the comparisonwise error rate, the Bonferroni  $t$ -tests were used to separate means. Because the adult survival experiment was terminated after 40 d and data contained right-censored observations, survival data were analyzed using the SAS LIFETEST procedure (SAS Institute 2003). Estimates of the survival distribution functions were computed using the product-limit (Kaplan–Meier) method. Generated survival curves for leafhoppers maintained on the selected plants were compared, and tests for homogeneity were performed. Also, 95% Hall–Wellner confidence bands were computed to compare the survival curves.

## Results

Leafhoppers were considered settled on host plant when they chose a spot on the plant and remained very still. At the beginning of this still period, they were often observed agitating and shaking both their hind legs and wings very fast as if they were trying to insert their stylets in the plant; however, because no EPG monitoring was used, there was no evidence that they were actually feeding. This behavior also was observed in the field (J.E.M., unpublished data). Overall, there was a significant difference between the mean numbers of leafhoppers settling on the studied plants over the 72-h experimental time ( $F = 150.68$ ;  $df = 5, 24$ ;  $P < 0.0001$ ). There was also a significant effect of time on the settling behavior of the leafhoppers ( $F = 7.70$ ;  $P < 0.0001$ ). In addition, results showed that there was a significant interaction effect between exposure time and plant species on the leafhopper settling behavior ( $F = 5.48$ ;  $P < 0.0001$ ). During the first 5 h of the settling behavior experiment, 60–100% of the leafhoppers remained arrested on the selected host plants (Table 1). During the first 2 h, leafhopper numbers significantly differed between host plants (Table 1). During the third hour, there was no statistical difference between the numbers of leafhoppers settling on the different host plants (Table 1), sug-

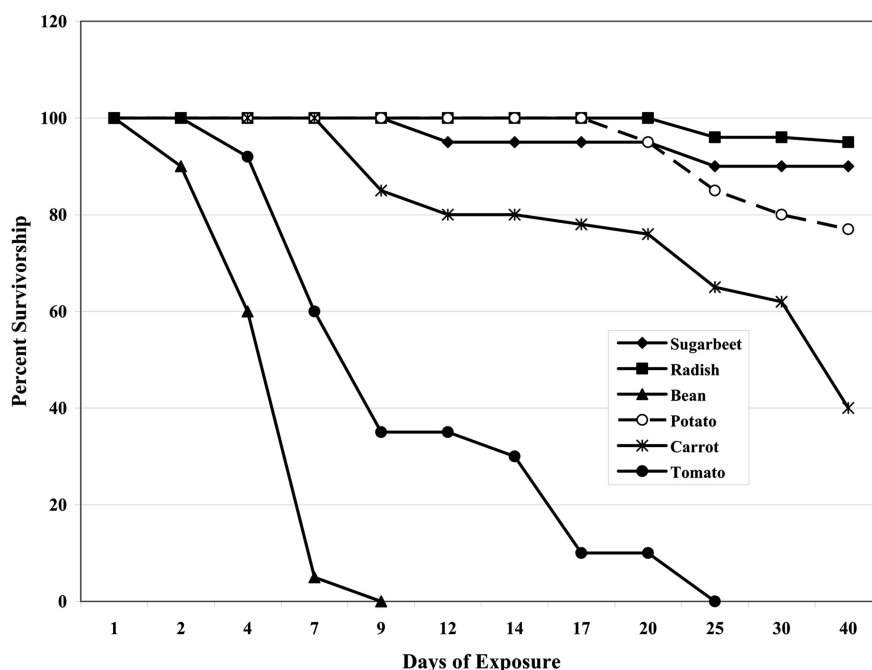


Fig. 1. Adult survivorship of beet leafhoppers confined on sugar beet, radish, bean, potato, carrot, and tomato plants for 40 d. Curves represent the mean of eight replications of twenty individuals each. The experiment was discontinued after 40 d.

gesting that there was no difference in plant acceptance. During the fourth hour, there was no significant difference between leafhoppers settled on sugar beet, radish, and potato or on carrot, tomato, and bean plants. However, after 4 h, numbers of leafhoppers settled on bean plants started to decline. After 24 h, leafhopper numbers had sharply declined for those settling on bean and tomato plants, and after 48 h, the trend continued. In contrast, the numbers of leafhoppers settling on sugar beet, radish, potato, and carrot plants stayed very high and steady until the end of the experimental period of 72-h exposure; however, the leafhoppers steadily settled on sugar beet, radish, and potato plants (Table 1). During this experiment, very few leafhoppers were observed resting or walking on the wall of cages containing sugar beet, radish, potato, and carrot plants.

Results of the overall comparison of leafhopper survival curves over the tested selected host plants (Fig. 1) indicated that there was a highly significant difference in the survivorship of the beet leafhoppers when confined on the different plants [Table 2;  $P < 0.0001$  for the log-rank test, Wilcoxon test, and likelihood ratio test,  $-2\text{Log(LR)}$ ]. Confidence intervals (Hall-Wellner confidence bands) to compare the survival curves were computed during the statistical analysis of the survival data. Unfortunately, the survival data did not provide good confidence interval estimates for most of the plants because of the high survival rates; thus, the confidence bands were not presented on the survival curve graph (Fig. 1). Comparisons among survival curves were instead performed separately using the rank tests for homogeneity of the PROC

LIFETEST to compare selected groups of curves. There was no significant difference between survival curves between sugar beet, radish, and potato plants ( $P = 0.1782$  for the log-rank test,  $P = 0.2038$  for the Wilcoxon test, and  $P = 0.1761$  for the likelihood ratio test). There was, however, a significant difference in leafhopper survivorship between sugar beet, radish, potato, and carrot plants ( $P < 0.0001$  for both the log-rank test and the Wilcoxon test, and  $P = 0.0002$  for the likelihood ratio test), suggesting that carrot is less suitable than the other three host plants. Results of the comparison of survival curves between carrot, tomato, and bean plants indicated that there was a highly significant difference ( $P < 0.0001$  for the log-rank test,

Table 2. Summary of the estimates of the tests of homogeneity of beet leafhopper survival curves over the selected host plants using the SAS LIFETEST procedure

Host plant	Rank statistics	
	Log-rank	Wilcoxon
Sugar beet	-10.774	-1012.0
Radish	-12.062	-1116.0
Potato	-7.850	-826.0
Carrot	0.657	-139.0
Tomato	13.535	1239.0
Dry bean	16.495	1854.0

Test of equality over the selected host Plants test			
	$\chi^2$	df	Pr > $\chi^2$
Log-rank	164.8740	5	<0.0001
Wilcoxon	150.0001	5	<0.0001
-2Log(LR)	159.5668	5	<0.0001



Wilcoxon test, and likelihood ratio test) between the curves. The survival curve for the tomato was different from that of carrot ( $P < 0.0001$  for the log-rank test, Wilcoxon test, and likelihood ratio test) and bean ( $P = 0.0001$  for the log-rank test,  $P = 0.0002$  for the Wilcoxon test, and  $P = 0.00027$  for the likelihood ratio test) survival curves.

Leafhopper mortality was high on bean and tomato plants, with almost all the leafhoppers confined on bean plants dying within about a week (Fig. 1). Most dead leafhoppers on bean plants were found stuck on plant hairs on the underside of leaves. The number of leafhoppers surviving on tomato plants dropped to  $\approx 35\%$  after 9 d and then declined gradually until all leafhoppers were dead after 25 d (Fig. 1). In contrast, there was no or little mortality on sugar beet and radish plants. There was almost no mortality to leafhoppers reared on potato plants up to  $\approx 17$  d, with few individuals dying gradually thereafter to end up with  $\approx 77\%$  of leafhoppers surviving after 40 d (Fig. 1). However, there was  $\approx 20\%$  mortality to leafhoppers maintained on carrot plants between 9 and 20 d after the confinement, with a sharp increase in mortality thereafter and reaching 60% at the end of the 40-d experimental period (Fig. 1).

Beet leafhopper oviposition and nymph production were only observed on sugar beet, radish, and potato plants. Leafhopper oviposition and nymph production occurred on all sugar beet and radish plants and six of the eight caged potato plants. Leafhopper eggs were found in 29 and 51 out of 34 and 58 leaves from sugar beet and radish plants, respectively. From a total of 86 potato leaves dissected, eggs were found in 44 leaves. However, the leaf dissection revealed the presence of desiccated eggs in seven potato leaves. The cause of these eggs desiccating and failing to hatch is unknown. Leafhopper nymphs produced on sugar beet, radish, and potato plants developed to the adult stage and more than one generation were produced until the experiment was discontinued after three months. No oviposition sites, eggs, or nymph production were observed on dry bean, tomato, or carrot plants.

### Discussion

In the current study, beet leafhoppers remained on all the presented host plants during the first four hours of the trials, but they departed from bean and tomato plants by the fifth and seventh hours of observations, respectively. These results suggest that bean and tomato plants would not be acceptable host plants for the beet leafhopper, whereas sugar beet, radish, potato, and carrot would be acceptable. Like Thomas (1972), we found that beet leafhopper does not discriminate between tomato and sugar beet during the first hour of exposure. He also pointed out that the beet leafhopper moves about randomly and is as likely to move to a nonaccepted as to an accepted host when first exposed to various plants.

Beet curly top virus can infect  $>300$  plant species (Thornberry 1966, Thomas 1969), whereas BLTVA phytoplasma is currently known to infect  $>40$  plant

species (Golino et al. 1989). Many of these plant species are not suitable hosts for the beet leafhopper, vector of both plant pathogens to several plants. It is not well understood how these plants are infected with pathogens by this leafhopper but its feeding behavior plays an important role in vectoring the pathogens. Although it was not possible to discern the actual feeding by the leafhoppers during the current study, because no EPG monitoring was conducted, beet leafhoppers did survive and reproduce on confined individuals of these plants for an extended time by feeding on them. BCTV and BLTVA infect both tomato and bean (Thomas 1969, Shaw et al. 1993, Lee et al. 2004a), yet both plants are not acceptable hosts for the beet leafhopper, the only insect known to vectoring both pathogens. Although the current study did not address any transmission studies of these pathogens, results of the present settling behavior study suggest that plants affected by the beet leafhopper-transmitted pathogens can be successfully inoculated in the first few hours of the leafhopper settling on these plants. Similar conclusions were reached by Thomas and Boll (1977) who showed that the beet leafhopper successfully transmitted BCTV as often to tomato as to sugar beet during the first hour of exposure. During this study, they also showed that percentage of BCTV transmission to tomato was twice as great as to sugar beet during the next 3 h; thereafter, transmission to sugar beet continued steadily, but transmission to tomato dropped off and nearly stopped 8 h after leafhopper confinement to these two host plants. Because this leafhopper seems to often depart from nonaccepted hosts to sample other plants, this settling and nibbling behavior may result in pathogen transmission to more plants, increasing disease spread within a field of nonaccepted plants.

There was high leafhopper mortality on bean and tomato plants after 4 d of exposure, suggesting again that these plants are not suitable hosts for the beet leafhopper. Similar results were reported by Thomas and Boll (1977) who indicated that leafhoppers confined on tomato began dying after 12–16 h, and few were alive after 72 h. The cause of leafhopper mortality on these nonaccepted hosts is not clear. Interestingly, most of the dead leafhoppers in bean-caged plants were found stuck on the underside of the leaves, which suggests that trichomes may have played an important role in the death. Survival was very high on sugar beet, radish, and potato until the end of the experiment, but carrot sustained leafhopper populations for only  $\approx 3$  wk. Because the present survival experiment was discontinued after 40 d, it was not possible to estimate the longevity of adult leafhoppers on all the different host plants studied. However, Meyerdirk and Moratorio (1987) reported that, with 95% confidence intervals, the longevity of the beet leafhopper adults reared on sugar beet varied with temperature and averaged 43.6–67.2 d (range 5–132 d) and 44.8–58.1 d (range 13–105 d) when maintained at constant temperatures ranging from 20 to 32°C for males and females, respectively. They also indicated that when maintained under fluctuating temperatures

of 19–36°C in the greenhouse, beet leafhopper females lived an average of 96.3 d with a longevity range of 65–142 d. Furthermore, Severin (1930) reported an adult beet leafhopper male to live as long as 126 d and a female 285 d.

Little is known on the beet leafhopper survival on other host plants. Information on survival of this leafhopper on various host plants is potentially important in designing effective management strategies to reduce the spread of pathogens transmitted by this insect. Insecticides are routinely used to control leafhoppers on several crops. It is possible to monitor beet leafhoppers using different tactics such as sweep sampling and yellow sticky traps. Although it may be possible to time the first insecticide applications, the number of applications during the growing season will depend on how long leafhoppers reside and survive in the crop.

During the current study, the beet leafhopper was able to reproduce on sugar beet, radish, and potato but not on bean and tomato. Also, although this leafhopper was able to survive on carrot, it failed to reproduce on this host plant. Not surprisingly, the beet leafhopper survived and reproduced on sugar beet (Severin 1930, Cook 1967, Meyerdirk and Moratorio 1987) and radish (J.E.M., unpublished data), these plants are considered very good hosts to this leafhopper. However, we did not expect the beet leafhopper reproducing and developing on potato, a plant previously thought to be an unacceptable host by this insect (Radcliffe 1982, Radcliffe et al. 1993). These results support previous observations in which beet leafhopper nymphs were commonly found in potato fields in Washington and Oregon (J.E.M., unpublished data). It is not clear whether these nymphs are produced within potato fields or whether they move into potatoes from weeds in the vicinity. During the current study, it was also found that some of the eggs laid by this insect in potato leaves failed to hatch; the cause of this egg mortality is unknown. Similar observations were reported for another leafhopper, *Macrostelus fascifrons* Stål, a species commonly found in potato fields and that transmits aster yellows phytoplasma, also causal agent of potato purple top disease. This leafhopper species feeds and lays eggs on potato, but for unknown reasons, these eggs fail to hatch (Radcliffe et al. 1993). It was also interesting to note that leafhoppers did so poorly on tomato, whereas the potato was fairly suitable for survival and reproduction of the beet leafhopper, despite that both host plants belong to the family Solanaceae.

In summary, results of the current study have implications in understanding how the beet leafhopper transmits various pathogens to several host plants that are not its accepted hosts. Information on settling behavior, survival, and reproductive response to various host plants is potentially important in designing effective management tactics to controlling this insect pest. This information can particularly help growers make good decisions on when and how long to apply insecticides to crops affected by pathogens vectored by this leafhopper. In addition, growers should avoid

growing sugar beet, radish, and potato in proximity. However, practical application of this knowledge may require further experimental work involving phytoplasma or virus transmission and insecticides to collect more data on this disease management issue.

## Acknowledgments

We are grateful to anonymous reviewers who made suggestions to an earlier draft of this manuscript. Financial support for this work was partially provided by the Washington State Potato Commission.

## References Cited

- Almeida, R.P.P., and E. A. Backus. 2004. Stylet penetration behaviors of *Graphocephala atropunctata* (Signoret) (Hemiptera, Cicadellidae): EPG waveform characterization and quantification. *Ann. Entomol. Soc. Am.* 97: 838–851.
- Backus, E. A., M. S. Serrano, and C. M. Ranger. 2005. Mechanisms of hopperburn: an overview of insect taxonomy, behavior, and physiology. *Annu. Rev. Entomol.* 50: 125–151.
- Bernays, E. A. 1996. Selective attention and host-plant specialization. *Entomol. Exp. Appl.* 80: 125–131.
- Bernays, E. A. 2001. Neural limitations in phytophagous insects: implications for diet breadth and evaluation of host affiliation. *Annu. Rev. Entomol.* 46: 703–727.
- Capinera, J. L. 2001. Handbook of vegetable pests. Academic, San Diego, CA.
- Cook, W. C. 1941. The beet leafhopper. U.S. Dep. Agric. Farmers' Bull. 1886.
- Cook, W. C. 1967. Life history, host plants, and migrations of the beet leafhopper in the western United States. U.S. Dep. Agric. Tech. Bull. 1365.
- Crosslin, J. M., J. E. Munyaneza, A. Jensen, and P. B. Hamm. 2005. Association of the beet leafhopper (Hemiptera: Cicadellidae) with a clover proliferation group phytoplasma in the Columbia Basin of Washington and Oregon. *J. Econ. Entomol.* 98: 279–283.
- DeLong, D. M. 1971. The bionomics of leafhoppers. *Annu. Rev. Entomol.* 16: 179–210.
- Golino, D. A., G. N. Oldfield, and D. J. Gumpf. 1989. Experimental hosts of the beet leafhopper-transmitted virescence agent. *Plant Dis.* 73: 850–854.
- Hills, O. A. 1937. The beet leafhopper in the central Columbia River breeding area. *J. Agric. Res.* 55: 21–31.
- Jung, H.-Y., Y. I. Hamh, J.-T. Lee, T. Hibi, and S. Namba. 2003. Characterization of a phytoplasma associated with witches' broom disease of potatoes in Korea. *J. Gen. Plant Pathol.* 69: 87–89.
- Lawson, F. R., J. C. Chamberlin, and G. T. York. 1951. Dissemination of the beet leafhopper in California. U. S. Dep. Agric. Tech. Bull. 1030.
- Lee, I.-M., K. D. Bottner, P. N. Miklas, and M. A. Pastor-Corrales. 2004a. Clover proliferation group (16SrVI) subgroup A (16SrVI-A) phytoplasma is a probable causal agent of dry bean phyllody disease in Washington. *Plant Dis.* 88: 429.
- Lee, I.-M., K. D. Bottner, J. E. Munyaneza, G. A. Secor, and N. C. Gudmestad. 2004b. Clover proliferation group (16SrVI) Subgroup A (16SrVI-A) phytoplasma is a probable causal agent of potato purple top disease in Washington and Oregon. *Plant Dis.* 88: 429.

- McLean, D. L., and W. A. Weight, Jr. 1968. An electronic measuring system to record aphid salivation and ingestion. *Ann. Entomol. Soc. Am.* 61: 180–185.
- Meyerdirk, D. E., and M. S. Moratorio. 1987. *Circulifer tenellus* (Baker), the beet leafhopper (Homoptera: Cicadellidae): laboratory studies on fecundity and longevity. *Can. Entomol.* 119:443–447.
- Miller, J. R., and K. Strickler. 1984. Plant-herbivore relationships: finding and accepting host plants, pp. 127–157. In W. J. Bell and R. T. Carde [eds.], *Chemical ecology of insects*, Chapman & Hall, London, United Kingdom.
- Munyanza, J. E. 2003. Leafhopper identification and biology, pp. 89–91. In *Proceedings of the 17th annual convention of the Pacific Northwest Vegetable Association*, 19–20 November 2003, Pasco, WA.
- Munyanza, J. E. 2004a. Leafhopper-transmitted diseases: emerging threat to Pacific Northwest potatoes, pp. 141–150. In *Proceedings of the University of Idaho Winter Commodity Schools–2004*, 20–22 January 2004, Pocatello, ID. University of Idaho Cooperative Extension System, Moscow, ID.
- Munyanza, J. E. 2004b. Leafhopper population dynamics in the south Columbia Basin, pp. 51–58. In *Proceedings of the 43rd Annual Washington State Potato Conference*, 3–5 February 2004, Moses Lake, WA.
- Munyanza, J. E., J. M. Crosslin, A. S. Jensen, P. B. Hamm, P. E. Thomas, H. Pappu, and A. Schreiber. 2005. Update on the potato purple top disease in the Columbia Basin, pp. 57–70. In *Proceedings of the 44th Annual Washington State Potato Conference*, 1–3 February 2005, Moses Lake, WA.
- O'Hayer, K. W., G. A. Schultz, C. E. Eastman, and J. Fletcher. 1984. Newly discovered plant hosts of *Spiroplasma citri*. *Plant Dis.* 68: 336–338.
- Radcliffe, E. B. 1982. Insect pests of potato. *Annu. Rev. Entomol.* 27: 173–204.
- Radcliffe, E. B., D. W. Ragsdale, and K. L. Flanders. 1993. Management of aphids and leafhoppers, pp. 127–157. In R. C. Rowe [ed.], *Potato health management*. American Phytopathological Society Press, St. Paul, MN.
- SAS Institute. 2003. SAS user's guide: statistics, version 9.1. SAS Institute, Cary, NC.
- Schultz, T. R., and M. E. Shaw. 1991. Occurrence of the beet leafhopper-transmitted virescence agent in red and daikon radish seed plants in Washington State. *Plant Dis.* 75: 751.
- Severin, H.H.P. 1928. Transmission of tomato yellows, or curly top of the sugar beet, by *Eutettix tenellus* Baker. *Hilgardia* 3: 251–275.
- Severin, H.H.P. 1929. Additional host plants of curly top. *Hilgardia* 3: 595–637.
- Severin, H.H.P. 1930. Life history of beet leafhopper, *Eutettix tenellus* (Baker) in California. *Univ. Calif. Publ. Entomol.* 5: 37–88.
- Shaw, M. E., D. A. Golino, and B. C. Kirkpatrick. 1990. Infection of radish in Idaho by beet leafhopper transmitted virescence agent. *Plant Dis.* 74: 252.
- Shaw, M. E., B. C. Kirkpatrick, and D. A. Golino. 1993. The beet leafhopper-transmitted virescence agent causes tomato big bud disease in California. *Plant Dis.* 77: 290–295.
- Smart, C. D., S. V. Thomson, K. Flint, and B. C. Kirkpatrick. 1993. The beet leafhopper transmitted virescence agent is associated with diseased potatoes in Utah. *Phytopathology* 83: 1399.
- Thomas, P. E. 1969. Thirty-eight new hosts of curly top virus. *Plant Dis.* 53: 548–549.
- Thomas, P. E. 1972. Mode of expression of host preference by *Circulifer tenellus*, the vector of curly top virus. *J. Econ. Entomol.* 65: 119–123.
- Thomas, P. E., and R. K. Boll. 1977. Effect of host preference on transmission of curly top virus to tomato by the beet leafhopper. *Phytopathology* 67: 903–905.
- Thomas, P. E., and M. W. Martin. 1971. Vector preference, a factor of resistance to curly top virus in certain tomato cultivars. *Phytopathology* 61: 1257–1260.
- Thornberry, H. H. 1966. Plant pests of importance to North American agriculture. In *Index of plant virus diseases*. U.S. Dep. Agric. Agric. Handb. 307.

Received 14 March 2005; accepted 15 August 2005.